

Results from the U.S. EPA's Biological Open Water Surveillance Program of the Laurentian Great Lakes: III. Crustacean Zooplankton

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ABSTRACT. Open water zooplankton communities were sampled across all five Laurentian Great Lakes during spring and summer 1998. Spring communities were characterized by relatively low species numbers and densities. Crustacean communities in all lakes except Lake Ontario were dominated by diaptomid copepods in spring. During summer, both abundance and species richness increased, the latter owing largely to the appearance of populations of cladocerans. Crustacean communities in the upper lakes were dominated by diaptomid copepods, cyclopoid copepodites, and *Daphnia galeata mendotae* (co-dominant with *Holopedium gibberum* in Lake Superior), and showed a high degree of spatial homogeneity. Lake Erie supported a notably more species rich community, and also exhibited a high degree of spatial heterogeneity. Lake Ontario differed from the other lakes by its relative lack of calanoid copepods, being dominated instead by cyclopoid copepods, along with *Bosmina* and *Daphnia*. There was a clear distinction between community composition in the western and eastern portions of the lake, though the reasons for this are unclear.

INDEX WORDS: Zooplankton, cladocerans, copepods, ecology, spatial distribution.

INTRODUCTION

Zoological studies of the Great Lakes date back over 100 years (Smith 1874, Forbes 1882, Forbes 1891, Marsh 1895, Jennings 1900, Eddy 1927, Ahlstrom 1936). Most of these early studies were either purely taxonomic or descriptive, often focusing on a small number of nearshore sites in one lake. In the past few decades an enormous body of work on zooplankton in the Great Lakes has developed, focusing both on structural and functional aspects of these communities. These studies, initially prompted by concerns about both nutrient enrichment of the lakes and changes in fish populations (cf. Fish and Assoc. 1960, Patalas 1969, Patalas

1972, Bradshaw 1964, McNaught *et al.* 1975, Watson and Wilson 1978) and more recently focusing on the impacts of non-indigenous invertebrate species (Lehman and Cáceres 1993, Branstrator 1995, MacIsaac *et al.* 1995) have led to an improved understanding of zooplankton communities in the Great Lakes. In spite of these advances in plankton research, descriptive studies comparing more than two lakes are still extremely rare. Schelske and Roth (1973), and later Robertson (1984), commented on the limited geographical scope of most Great Lakes research, and the consequent lack of multi-lake comparative studies. While a number of studies have examined zooplankton distributions in more than one lake, they have drawn from data collected in different years (Wat-

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TABLE 1. Minimum, maximum, and mean depths (m) of zooplankton sampling stations. Station depths for Lake Erie are shown by basin (W = western basin; C = central basin; E = eastern basin).

	Superior	Michigan	Huron	Erie - W	Erie - C	Erie - E	Ontario
Minimum	90.0	89.0	51.0	7.5	20.9	32.6	52.5
Maximum	290.0	257.0	133.8	10.0	24.3	62.7	191.0
Average	180.2	141.5	89.3	8.8	22.7	47.5	125.8

son and Carpenter 1974), or indeed from different studies (Sprules and Jin 1990). In these cases, questions of comparability of data inevitably occur, especially considering the wide variation in zooplankton collection and enumeration techniques often used. To date, there appear to be no published reports on comparative zooplankton distribution across all five Laurentian Great Lakes taken from a single survey.

The Great Lakes National Program Office (GLNPO) of the United States Environmental Protection Agency (U.S. EPA) has conducted surveillance monitoring of the offshore waters of the Great Lakes since 1983. The monitoring effort is focused on the relatively homogeneous offshore waters of each lake, and provides extensive coverage of all five lakes during two well-defined yearly periods: the spring isothermal period and the stable, stratified summer period. In addition to a wide range of physical and chemical parameters, the lakes are currently sampled for phytoplankton, zooplankton, and benthic invertebrates. This sampling program is unique in that all five lakes are sampled concurrently by one agency, and samples are analyzed by one primary lab. Consequently, analytical methods, and most importantly taxonomy, remain consistent both over time and across all five lakes.

In this series of papers we are presenting, for the first time, data covering all five Laurentian Great Lakes from GLNPO's biological surveillance sampling program. The goals in this series of papers are threefold: 1) to provide a general description of the offshore planktonic and the benthic communities of all five Great Lakes; 2) to identify large-scale patterns of distribution of these communities; and 3) to identify the potential physical and chemical factors controlling the species makeup of these communities. Previous papers have dealt with epilimnetic phytoplankton (Barbiero and Tuchman 2001a) and the deep chlorophyll maximum (Barbiero and Tuchman 2001b). Here the distribution and abundance of crustacean zooplankton in the Laurentian Great Lakes are examined.

METHODS

Samples were collected for zooplankton analysis during the spring and summer cruise, 1998, during which a total of 72 stations were sampled. Station locations and sampling dates are presented elsewhere (Barbiero and Tuchman 2001a); information on station depths is provided in Table 1. The choices of methodology and data presentation, when collecting comparative zooplankton samples in water bodies with such widely varying depths on a research vessel with 24 hour operations, are somewhat problematic. Historically, GLNPO has sampled zooplankton using a metered, conical, 0.5 m diameter (D:L = 1:3), 64 μ m mesh net to a depth of 20 m (or 1 m above the bottom at shallower stations). However, it is well known that many crustacean species in the Great Lakes undertake diurnal migrations that can take them below 20 m during the day, and in some cases, particularly in the case of some of the larger calanoid copepods, the majority of the population can remain below this depth at all times (Wells 1960, Patalas 1969, Wilson and Roff 1973). GLNPO data show that daytime population maxima of most crustaceans in Lakes Michigan, Erie, and Ontario typically occur between 20 and 40 m, while the widely-distributed calanoid copepods *Limnocalanus macrurus* and *Leptodiaptomus sicilis* rarely ascend above 20 m at any time (GLNPO, unpublished data). Shallower (20 m) tows thus can provide grossly inaccurate indications of crustacean community composition, particularly when taken during the day. Therefore, in 1997 GLNPO added a second zooplankton tow to its sampling routine, which was taken to a depth of 100 m (or 2 m above the bottom at stations < 100 m), using a metered, 153 μ m mesh net. The larger mesh size was used to avoid problems with clogging. Comparisons between samples collected during the summer of 1998 using the two mesh sizes at 12 stations in the western and central basins of Lake Erie shallower than 20 m found a significant difference in only one (*Mesocyclops* copepodites) of the 24 crustacean groups examined (GLNPO, unpublished data).

Reliance on data from 100 m tows, however, precludes the use of volumetric ($\#/m^3$) units, since individuals are unlikely to be evenly distributed throughout this depth. In particular, densities of most species will be lower throughout the deeper portions of the tow, resulting in a negative bias in density estimates of deeper stations, in comparison to shallower stations, when numbers are integrated over the depth of the tow. In light of these considerations, in this paper results are presented from deep tows, and these data are reported primarily in areal units ($\#/m^2$) to facilitate comparisons between stations of different depths. Volumetric densities of major groups are also presented to enable comparisons with previous studies, though it should be borne in mind that these data integrate the numbers of organisms over the entire water column sampled.

After collection, samples were immediately narcotized with soda water, and preserved with sucrose formalin solution (Haney and Hall 1973) approximately 20 minutes later. Samples were split in the lab using a Folsom plankton splitter, and four stratified aliquots examined per sample using a stereoscopic microscope.

Crustacean taxonomy largely followed Balcer *et al.* (1984); other keys consulted included Hudson *et al.* (1998), Brooks (1957), Evans (1985), and Rivier (1998). Immature calanoids and cyclopoids were identified to the lowest taxonomic level possible, usually suborder or genus. Nauplii are enumerated in separate counts, and those data will not be reported here. Length measurements were made on the first twenty individuals of each species encountered per sample.

Patterns in zooplankton community composition across the lakes were explored with the use of detrended correspondence analysis, using the program CANOCO v 4.0. Analysis was restricted to the summer survey due to very low species richness in the spring. To ensure units were commensurate with those of environmental factors, volumetric density estimates of crustaceans, excluding *Mysis*, were used, with replicate tows treated as separate samples. Densities were converted to natural logarithms to reduce the undue influence of a few dominant species. To help identify the environmental gradients associated with the ordination axes, correlations were calculated between axis scores for each sample and the following environmental variables: chloride, chlorophyll *a*, temperature, total soluble phosphorus, total phosphorus, depth, dissolved silica, conductivity, alkalinity, turbidity, nitrate + nitrite, chloride, particulate phosphorus, particulate

nitrogen, and particulate carbon. The resulting correlation coefficients were plotted against axis scores, and the relationships between environmental variables and ordination axes were represented in ordination space as lines, with the angle of the line indicating the degree of correlation with the two axes, and the length of the line indicating the strength of that correlation. Analytical methods for the measurement of the environmental variables, as well as ranges of most of these variables for the five lakes, are provided elsewhere (Barbiero and Tuchman 2001a).

RESULTS

Spring

On an areal basis, average lake-wide densities of crustaceans during the spring were very similar for Lakes Michigan, Huron and Ontario (300,081, 304,847, and 238,495/ m^2 , respectively; Table 2), while densities in Lake Superior were substantially lower (average = 63,505/ m^2). No obvious trends in spatial heterogeneity within these lakes were apparent (Fig. 1). Total crustacean densities in Lake Erie, on the other hand, varied by more than two orders of magnitude, ranging from 579/ m^2 at a station in the eastern basin to over 80,000/ m^2 in the central basin. This spatial variability was more pronounced when considered on a volumetric basis, in which case densities ranged from a low of 19/ m^3 at a station in the eastern basin to over 6,000/ m^3 in the western basin. While densities in the eastern basin were uniformly low, those within both the central and western basins were highly variable. A similarly high amount of intra-basin variability was seen in phytoplankton biomass in spring (Barbiero and Tuchman 2001a). A forward selection stepwise multiple regression was conducted on ln-transformed zooplankton density and available physical and chemical variables, using SYSTAT 5.02, to determine possible causes for the variability in densities in Lake Erie. To ensure comparable units, volumetric densities ($\#/m^3$) were used. Both temperature and chlorophyll were identified as significant variables; the resulting relationship was highly significant (Table 3). Inspection of the individual relationships between the two variables and zooplankton abundance, however, suggested that temperature was correlated primarily with inter-basin differences, while chlorophyll was correlated with intra-basin differences only within the central basin (Fig. 2).

Copepods dominated the crustacean communities

TABLE 2. Average lake-wide densities (individuals/m²) of crustacean zooplankton taxa during spring survey, 1998. + indicates < 1/m². Numbers in parenthesis indicate volumetric densities (#/m³). Densities for the three basins of Lake Erie (W = western, C = central, E = eastern) are shown separately.

	SU	MI	HU	ER-W	ER-C	ER-E	ON
Cladocera							
<i>Diaphanosoma birgei</i>				1			
<i>Daphnia galeata mendotae</i>	21		74	515	407	1	433
<i>Daphnia longiremis</i>					24		
<i>Daphnia retrocurva</i>					1		
<i>Bosmina longirostris</i>			78	307	2,207	19	400
<i>Eubosmina coregoni</i>				12	694	1	474
<i>Macrothrix</i> spp.						1	
<i>Alona</i> spp.				16	3	1	
TOTAL Cladocera	21		152	850	3,336	24	1,307
	(0.2)	(0.0)	(2.2)	(98.2)	(161.1)	(0.6)	(13.9)
Copepoda							
Calanoida							
<i>Senecella calanoides</i>	47	233	275				
<i>Senecella</i> copepodites	264						
<i>Limnocalanus macrurus</i>	1,318	1,742	3,677	311	+		581
<i>Limnocalanus</i> copepodites	11,908	251	5,787	1,421			10,702
<i>Epischura</i> copepodites	11						170
<i>Eurytemora</i> copepodites							47
<i>Leptodiaptomus ashlandi</i>	24	102,684	93,070	6,688	144	8	
<i>Leptodiaptomus minutus</i>		22,731	29,133	1,994	554	66	264
<i>Leptodiaptomus sicilis</i>	29,185	24,520	31,684	2,400	13		2,966
<i>Skistodiaptomus oregonensis</i>		263	228	14	2,771	18	1,461
Diaptomid copepodites	1,086	131,377	112,790	3,947	61	11	29,397
TOTAL Calanoida	43,841	283,803	276,644	16,775	3,542	103	45,588
	(443.5)	(2,921.0)	(3,676.5)	(2,042.2)	(173.6)	(2.2)	(528.8)
Cyclopoida							
<i>Diaicyclops thomasi</i>	16,621	10,013	16,928	1,368	12,197	97	122,901
<i>Acanthocyclops vernalis</i>				39			
<i>Diaicyclops nanus</i>				12	8		
<i>Eucyclops agilis</i>				31			
Cyclopoid copepodites	3,006	5,624	10,935	1,449	10,194	3,445	68,144
<i>Mesocyclops edax</i>	7			8	3		
<i>Mesocyclops</i> copepodites				1			
<i>Tropocyclops prasinus mexicanus</i>	9	641	176	11	696	184	556
<i>Tropocyclops</i> copepodites				1			
TOTAL Cyclopoida	19,643	16,278	28,038	2,921	23,099	3,727	191,601
	(198.2)	(167.5)	(379.3)	(348.8)	(1,124.7)	(77.2)	(2,128.0)
Harpacticoida							
Harpacticoid spp.			13	337	152	44	
TOTAL	63,505	300,081	304,847	20,884	30,130	3,897	238,495
	(641.9)	(3,088.6)	(4,058.2)	(2,530.2)	(1,467.0)	(80.8)	(2,670.7)

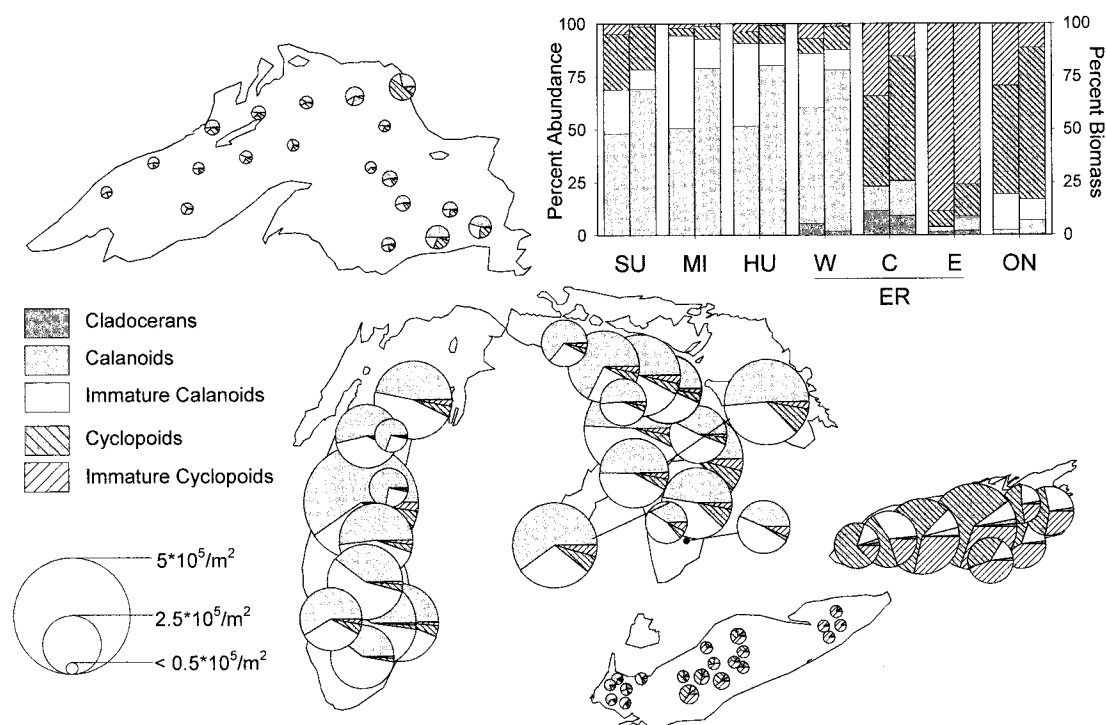


FIG. 1. Areal densities ($\#/m^2$) of major crustacean groups, spring survey, 1998. Insert shows whole-lake average percent composition in terms of abundance (left bars) and biomass (right bars). Lake Erie is broken down by basin (W = western basin, C = central basin, E = eastern basin).

in all five lakes during the spring (Fig. 1). Immature copepods made up a substantial portion of individuals at all stations, although the relative importance of calanoids and cyclopoids varied from lake to lake. Adult animals in Lakes Michigan and Huron

TABLE 3. Results of multiple regression between \ln transformed zooplankton abundance ($\#/m^3$) and temperature and chlorophyll concentration for Lake Erie, spring survey.

Variable	Coefficient	SE	<i>t</i>	P(2 Tail)
Constant	3.052	0.976	3.128	0.006
Temp	0.462	0.192	2.408	0.028
Chl	0.494	0.179	2.759	0.013

Adjusted $r^2 = 0.431$

Analysis Of Variance

Source	SS	DF	MS	F	P
Regression	24.03	2	12.02	8.18	0.003
Residual	24.96	17	1.47		

were predominantly calanoids, while Lake Ontario was dominated by cyclopoid copepods. Dominance varied from station to station in Lake Erie, and in Lake Superior calanoids and cyclopoids were co-dominant at most stations. As might be expected, when looked at in terms of biomass, the contribution of adult organisms was proportionally greater than that of immatures. This was particularly the case for the calanoid copepods.

Species richness of the crustacean communities on a station by station basis was low, with most stations supporting between 5 and 10 species; in Lake Superior no more than 6 taxa were found at any station (Table 4). Total numbers of taxa found in each lake ranged from 9 (Lake Superior) to 20 (Lake Erie) and were largely confined to a small number of species belonging to one or a few genera. The calanoids *Leptodiaptomus ashlandi*, *Leptodiaptomus sicilis*, and *Leptodiaptomus minutus*, and immatures of this genus, accounted for most of the organisms found in Lakes Michigan and Huron (Table 2). These two lakes were extremely similar, both in terms of community composition and of the

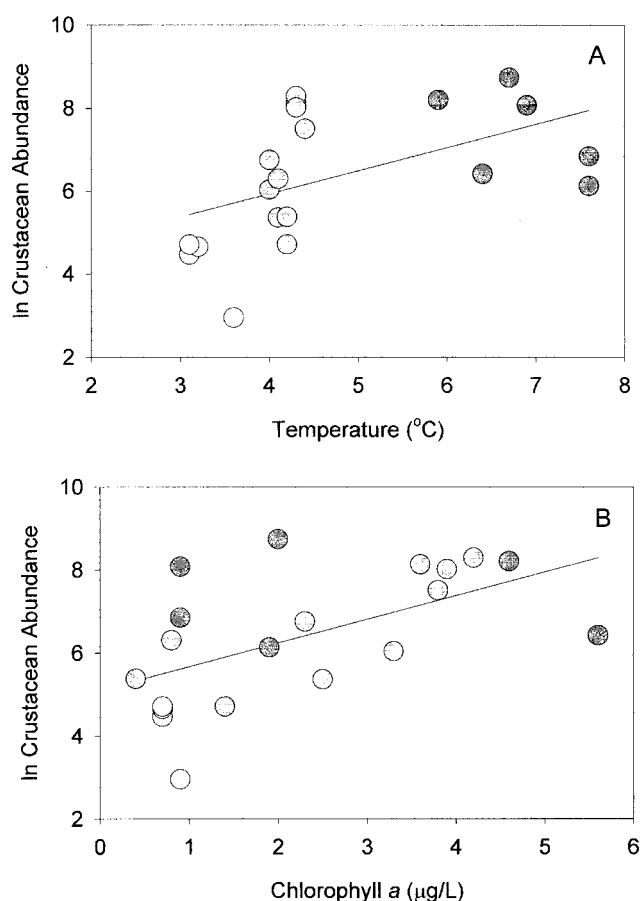


FIG. 2. Relationship between \ln transformed zooplankton density ($\#/m^3$) and A.) Temperature; and B.) Chlorophyll *a* concentration for all stations in Lake Erie, spring survey, 1998. ○ = eastern basin; ◐ = central basin; ● = western basin.

TABLE 4. Numbers of crustacean taxa found per station, and total taxa found per lake.

Spring Survey					
	Superior	Michigan	Huron	Erie	Ontario
Minimum	3	6	6	7	5
Maximum	6	8	9	14	9
Mean	5	7	7	10	7
Total	9	8	11	20	11
Summer Survey					
	Superior	Michigan	Huron	Erie	Ontario
Minimum	8	9	10	10	8
Maximum	14	14	16	19	17
Mean	9	12	12	14	12
Total	16	16	17	27	19

absolute densities of the constituent species. Lake Ontario was dominated by the cyclopoid *Diacyclops thomasi* and immature cyclopoids. Most stations in Lake Superior supported a mix of *L. sicilis*, *D. thomasi*, and immatures of the calanoid genus *Limnocalanus*. In Lake Erie, substantial populations of both *D. thomasi* and *L. ashlandi* were found in the western and central basins, in addition to smaller populations of *L. minutus*, *L. sicilis*, *Skistodiaptomus oregonensis*, and immatures of *Limnocalanus* and the cladoceran *Bosmina longirostris*. Stations in the eastern basin were composed almost entirely of very small populations of immature cyclopoids.

Summer

Total crustacean densities during the summer were substantially higher than in spring in all lakes (Table 5, Fig. 3). The most dramatic increases were seen in the central and eastern basins of Lake Erie, where densities increased on average 11 and 104 times, respectively, and in the western stations in Lake Ontario where densities were about 20 times greater than in spring. Lesser, but still substantial, increases were seen in the upper lakes.

Between-lake differences in average lake-wide densities were more pronounced in summer than in spring. Areal densities in Lake Ontario averaged nearly $2.5 \times 10^6/m^2$, over double that of Lake Huron, the lake with the second highest average density. Due to its shallowness, the western basin of Lake Erie had the lowest areal densities of crustaceans, but on a volumetric basis densities were nearly as high as in Lake Ontario (Table 5). Average areal abundance in Lake Superior were approximately half that in Lake Michigan, and one third that of Lake Huron.

The most significant change in the summer crustacean communities was an increase in the importance of cladocerans, largely members of the genera *Daphnia*, *Bosmina*, and *Eubosmina*. As a result, species richness of the crustacean community was substantially higher during the summer, compared to spring, with most stations supporting between 9 and 15 species. Total numbers of taxa found in each lake ranged from 16 to 27, with Lake Erie supporting the greatest number of species (Table 4). Even so, most lakes were still dominated by a relatively small number of species.

On a lake-wide basis, diaptomid copepodites were one of the dominant groups in all lakes but Ontario, where instead cyclopoid copepodites pre-

TABLE 5. Average lake-wide densities (individuals/m²) of crustacean zooplankton taxa during summer survey, 1998. Numbers in parenthesis indicate volumetric densities (#/m³). Densities for the three basins of Lake Erie (W = western, C = central, E = eastern) are shown separately.

	SU	MI	HU	ER-W	ER-C	ER-E	ON
Cladocera							
<i>Bythotrephes cederstroemi</i>	294	181	515	6	1,688	509	
<i>Cercopagis pengoi</i>							2,473
<i>Leptodora kindtii</i>	14	236		2,882	31	713	2,529
<i>Polyphemus pediculus</i>							1,333
<i>Diaphanosoma birgei</i>				5,391		149	36
<i>Holopedium gibberum</i>	19,909		645	34			1,071
<i>Ceriodaphnia</i> spp.				17			
<i>Daphnia galeata mendotae</i>	19,502	232,105	235,504	473	57,906	8,468	4,399
<i>Daphnia longiremis</i>			169	71	1,285	1,200	
<i>Daphnia pulex</i>	32					871	
<i>Daphnia retrocurva</i>				17,678		880	605,504
<i>Eubosmina coregoni</i>		229	8,487	68,795	2,267	182	44,474
<i>Bosmina longirostris</i>	2,375	9,730	61,369	21,455	7,394	171,994	902,381
Total Cladocera	42,126	242,482	306,689	116,802	70,571	184,966	1,564,201
	(423)	(2,493)	(3,938)	(14,036)	(3,431)	(3,655)	(17,035)
Copepoda							
Calanoida							
<i>Senecella calanoides</i>	1,163	208	168		23		
<i>Senecella copepodites</i>			109				
<i>Limnocalanus macrurus</i>	19,398	11,009	12,611		35		22,145
<i>Limnocalanus copepodites</i>	60	343	544		54		
<i>Epischura lacustris</i>	190	2,361	3,302	91	5,965	9,916	865
<i>Epischura copepodites</i>	262	4,538	6,014	430	11,372	31,428	870
<i>Eurytemora affinis</i>				1,456		149	1,494
<i>Eurytemora copepodites</i>							73
<i>Leptodiaptomus ashlandi</i>	62	22,757	35,764	69	6,223	303	
<i>Leptodiaptomus minutus</i>	17	9,767	27,687	1,282	8,716	6,464	1,095
<i>Leptodiaptomus sicilis</i>	14,362	63,997	34,005	570	584	245	16,669
<i>Leptodiaptomus siciloides</i>	41			2,710	64	76	
<i>Skistodiaptomus oregonensis</i>		1,072	267	1,436	44,925	35,181	5,029
Diaptomid copepodites	195,598	190,817	268,337	27,326	88,353	76,352	26,107
Total Calanoida	231,153	306,869	388,808	35,371	166,313	160,115	74,348
	(2,326)	(3,162)	(5,072)	(4,253)	(8,104)	(3,702)	(805)
Cyclopoida							
<i>Acanthocyclops vernalis</i>				3,218		459	
<i>Diaconocyclops thomasi</i>	22,764	20,132	28,408	151	4,884	3,011	203,804
<i>Eucyclops agilis</i>				217			
Cyclopoid copepodites	59,005	85,025	204,009	10,279	60,166	22,575	648,270
<i>Mesocyclops edax</i>	33	846	169	8,384	14,097	3,693	77
<i>Mesocyclops copepodites</i>	17	953	49	5,477	17,451	4,962	
<i>Tropocyclops prasinus mexicanus</i>		1,233	42	462	2,406	23,193	749
<i>Tropocyclops copepodites</i>		1,010		78	1,546	6,192	730
Total Cyclopoida	81,819	109,199	232,677	28,266	100,550	64,084	853,631
	(8,210)	(1,117)	(3,090)	(3,535)	(4,890)	(1,434)	(9,444)
Harpacticoida							
Harpacticoid spp.				14			
TOTAL	355,098	658,550	928,173	180,454	337,435	409,165	2,492,180
	(3,571)	(6,772)	(12,100)	(21,827)	(16,424)	(8,791)	(27,284)

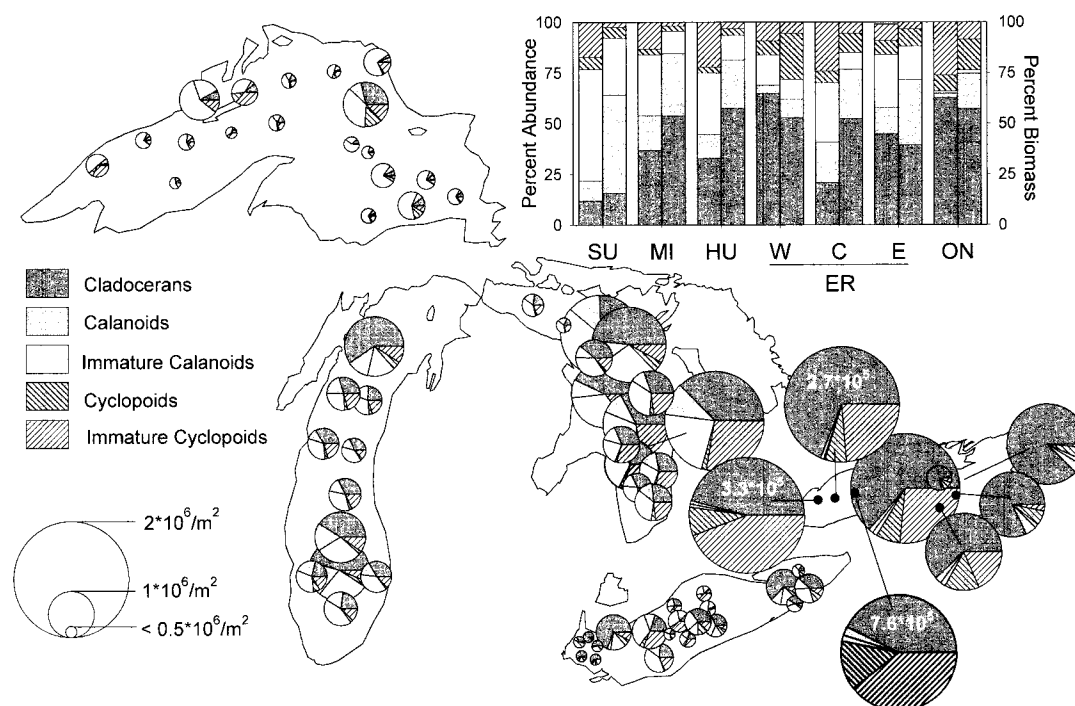


FIG. 3. Areal densities ($\#/m^2$) of major crustacean groups, summer survey, 1998. Insert shows whole-lake average percent composition in terms of abundance (left bars) and biomass (right bars). Lake Erie is broken down by basin (W = western basin, C = central basin, E = eastern basin).

dominated. When relative contributions of the major groups are considered in terms of biomass, the importance of adult calanoid copepods increases, particularly in those areas (Lakes Superior, Michigan, Huron) supporting the cold-water, larger bodied forms *L. macrurus* and *L. sicilis*. Adult copepods in Lake Superior were for the most part evenly divided into the following three species: *L. sicilis*, *L. macrurus*, and *D. thomasi* (Table 5). Lakes Michigan and Huron supported extremely similar copepod communities. As in spring, the diaptomids *L. ashlandi*, *L. minutus*, and *L. sicilis* were predominant, with *L. macrurus* and *D. thomasi* also present in substantial numbers. Lake Erie had the most diverse copepod community during the summer, although species distribution exhibited a high degree of spatial heterogeneity. A number of species found in Lake Erie were present in either very limited numbers or not at all in the other five lakes, among them *S. oregonensis*, *Eurytemora affinis*, *Leptodiaptomus siciloides*, *Acanthocyclops vernalis*, *Eucyclops agilis*, *Mesocyclops edax*, and *Tropocyclops prasinus mexicanus*. Copepods were most dominant in the central basin,

where they comprised 80% of individuals; this basin also had the largest percentage of cyclopoids. In the eastern basin, copepods contributed somewhat more than half the individuals, with calanoids twice as abundant as cyclopoids, while copepods were least dominant in the western basin, contributing less than 40% of individuals, and were equally divided between the two suborders. Lake Ontario was unique in the dominance of its copepod communities by cyclopoids. While the majority of these were immatures, adults were almost exclusively of the species *D. thomasi*.

Dominant cladocerans varied from lake to lake and, in the lower lakes, from basin to basin (Table 5). Cladocerans were least numerous in Lake Superior, where they were represented mostly by *Daphnia galeata mendotae* and *Holopedium gibberum*. *D. galeata mendotae* was the dominant cladoceran in Lakes Michigan and Huron, contributing 35 and 25% of individuals in the two lakes, respectively. As in spring, a greater degree of spatial heterogeneity in community composition was found in Lake Erie, and dramatic differences in community composition were also found between different stations

in Lake Ontario. *B. longirostris*, present to some degree in all five lakes, dominated the western and eastern basins of Lake Erie, as well as the western basin of Lake Ontario, while in the central basin of Lake Erie the dominant cladoceran was *D. galeata mendotae*. In the eastern basin of Lake Ontario, numbers of *Bosmina* were greatly reduced in comparison to the western basin, and its place was apparently taken by *Daphnia retrocurva*, an organism otherwise found in substantial numbers only in western Lake Erie.

Three major predatory cladocerans were found in the lakes: the native *Leptodora kindtii*, a recent invader *Bythotrephes cederstroemi*, and *Cercopagis pengoi*, which appeared in the lakes for the first time in 1998. Of the three, *Bythotrephes* was the most widely distributed, being recorded from 41 of the 72 stations sampled (Fig. 4). It was present in all lakes with the exception of Lake Ontario, and attained its highest populations in the central basin of Lake Erie. The distribution of *Leptodora* was much more restricted, although it achieved a maximum abundance more than double that of *Bythotrephes*. It was notably absent from Lake Huron, and appeared in limited numbers at few stations in Lake Michigan. Interestingly, its distribution showed little overlap with that of *Bythotrephes*, with substantial numbers of individuals found in the western basin of Lake Erie and in Lake Ontario. *Cercopagis pengoi* was first noted in Lake Ontario in late July of 1998 (MacIsaac *et al.* 1999), and during the summer survey was restricted to four stations in the eastern basin of the lake.

DCA ordination of the summer crustacean data resulted in very clear separation of all lakes except Lakes Michigan and Huron, which together formed a tight cluster (Fig. 5). Both Lakes Erie and Ontario formed more diffuse groupings, with the three basins of Lake Erie exhibiting no overlap with each other, and the western and eastern basins of Lake Ontario similarly separated. The positions of Lakes Superior, Michigan/Huron, and the central and eastern basins of Lake Erie strongly implied a diagonal positively correlated to both axes and with a slope close to 1. Correlations with environmental variables showed that this diagonal was most strongly associated with increasing depth and silica concentration, and decreasing temperature, conductivity, pH, and alkalinity. A second diagonal, roughly perpendicular to the first and most strongly associated with phosphorus and chlorophyll, served to separate the western basin of Lake Erie from the rest of the lake at the lower end of the primary diagonal, and

Lake Ontario from Lake Superior at the upper end of the primary diagonal. It is interesting that all three upper lakes were at the extreme low end of this second, phosphorus-associated diagonal, and thus did not appear to be differentiated from each other by it. Total phosphorus values for western Lake Erie and Lake Ontario were indeed notably higher (\bar{x} = 10.2, SD = 2.5 $\mu\text{g P/L}$) than those for other areas of the lakes (\bar{x} = 4.1, SD = 1.2 $\mu\text{g P/L}$), which did not differ that substantially from each other. Similar, though less consistent, differences were seen for chlorophyll concentrations (western Erie and Ontario: \bar{x} = 2.03, SD = 0.96 $\mu\text{g Chl a/L}$; other areas: \bar{x} = 0.55, SD = 0.34 $\mu\text{g Chl a/L}$)

DISCUSSION

Species Richness

During this study, 35 crustacean taxa were found in the open waters of the Great Lakes. However, 99% of the individuals found during spring and summer came from 8 and 14 species, respectively. Gannon (1981), commenting on the high species diversity of crustacean communities in the Great Lakes, suggested that it was not unusual to collect 20 crustacean species in a single vertical tow. This was not the case in this study, where average numbers of taxa per station for the five lakes ranged between 5 and 10 during spring and 9 and 14 during summer. The species found during this study were substantially similar to those previously reported for the lakes by Watson (1974); of the 25 species he listed from the five Great Lakes, 19 appear on the species list for this study (taking into account nomenclatural changes). Of the crustaceans listed by Watson but not found in this survey, *Chydorus sphaericus* is primarily a littoral or benthic cladoceran which has been reported from all five lakes but has historically been more common in Lake Erie (Balcer *et al.* 1984), while the calanoid *Osphranticum labronectum*, and the daphnids *D. parvula*, *D. ambigua*, and *D. pulex* have been reported by various authors as either rare and/or taxonomically ambiguous (Selgeby 1975, Balcer *et al.* 1984, Evans 1985). *Daphnia pallidus*, included in Watson's list, seems to have appeared in only one report (Patalas 1972). Patalas (1975), in a study classifying 14 North American great lakes on the basis of crustacean communities, grouped Lakes Superior and Huron together in part on the basis of high species number (18 to 23), while Lakes Erie and Ontario were grouped on the basis of intermediate species number (11 to 18). Lake Michigan

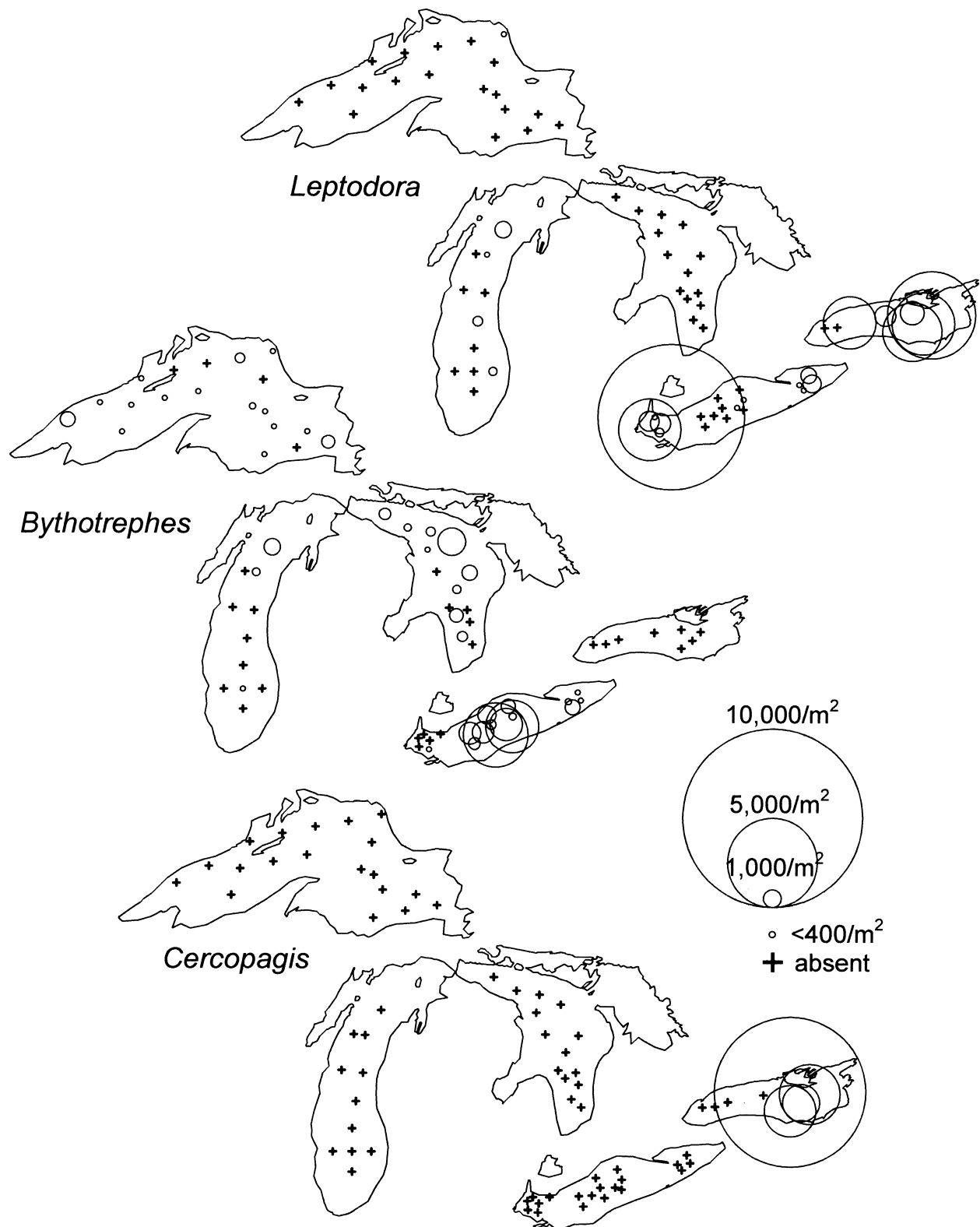


FIG. 4. Areal densities (#/m²) of predatory cladocerans in the Great Lakes during summer survey, 1998.

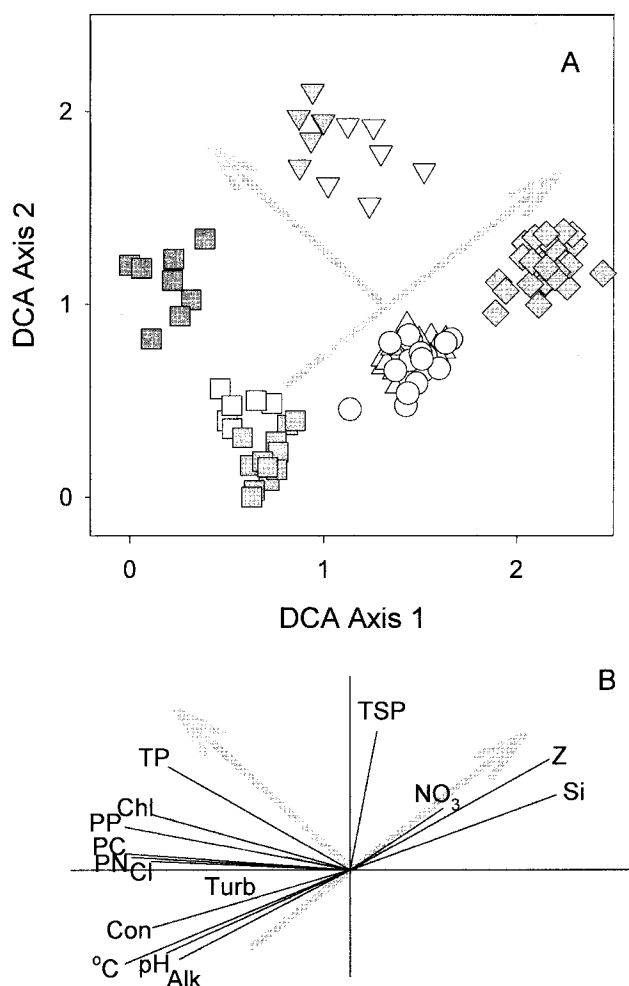


FIG. 5. A.) Results of detrended correspondence analysis of spring 1998 crustacean data (\diamond = Superior; \circ = Michigan; \triangle = Huron; \blacksquare = Erie, central basin; \blacksquare = Erie, western basin; \blacktriangledown = Ontario eastern basin; \triangledown = Ontario, western basin. B.) correlations of environmental variables with ordination axis scores. The angle of the line indicates the degree of correlation with the two axes, and the length of the line indicates the strength of that correlation. Cl = chloride; Chl = chlorophyll *a*; $^{\circ}\text{C}$ = temperature; TSP = total soluble phosphorus; TP = total phosphorus; Z = depth; Si = dissolved silica; Con = conductivity; Alk = alkalinity; Tur = turbidity; NO_3 = nitrate and nitrite; Cl = chloride; PP = particulate phosphorus; PN = particulate nitrogen; PC = particulate carbon. Gray arrows indicate diagonals implied by groupings of stations.

shared characteristics of both of these groups. These data, however, would suggest that all the lakes have similar numbers of species except for Lake Erie, which supports the most species-rich community.

Spatial Distribution

Very few studies have been carried out to date on the offshore waters of the Great Lakes with sufficient spatial coverage to address the question of large-scale horizontal variation in zooplankton communities. Most previous studies have focused on either nearshore/offshore differences (Swain *et al.* 1970, Taylor *et al.* 1987) or smaller, well-circumscribed water bodies such as Saginaw Bay (Stemberger *et al.* 1979), the Straits of Mackinac (Gannon *et al.* 1976) or Green Bay (Sager and Richman 1991). Minns (1984) compiled zooplankton data from a number of surveys and used a statistical model to determine spatial variability in all of the lakes except Lake Michigan. He found that the open lake communities were largely uniform, with most spatial differences resulting from nearshore/offshore differences. Watson and Wilson (1978), in an extensive survey of Lake Superior, found the open waters to be largely homogeneous during most of the year, as determined by cluster analysis. Spatial heterogeneity was most apparent during September and October, when most midlake stations fell into two and three clusters, respectively. Similarly, the data from this study suggest that distributions of species were largely homogeneous in the open waters of each of the upper lakes. This is most strongly demonstrated by the extremely tight clustering of stations in the DCA.

The lower lakes, in contrast, exhibited a substantial degree of spatial heterogeneity, primarily along an east-west axis in both lakes. Distinctions between zooplankton communities in the three basins of Lake Erie are well known (Davis 1969, 1968), and are not surprising given the substantial differences in morphometric and trophic characteristics of the different basins. In this study, a high degree of spatial heterogeneity was also seen within basins, specifically the western and central basins and particularly, but not exclusively, in the spring. This heterogeneity was apparent both in vastly differing densities and differences in species composition. Stockwell and Sprules (1995) have also documented substantial spatial heterogeneity of zooplankton biomass in Lake Erie, using an optical plankton counter. They suggested that temperature

was most important in determining spatial patterns of biomass. Patalas (1969) had similarly found a strong positive correlation between zooplankton abundance and heat content in Lake Ontario. In this study the effects of temperature seemed largely confined to inter-basin variability, while intra-basin variability in abundance, at least in the central basin, was associated with differences in chlorophyll concentration. Current patterns in Lake Erie tend to be complex (Beletsky *et al.* 1999), with the central basin in particular often divided into a number of circulation cells, as appears to have been the case during both the spring and summer surveys (unpubl. data, Great Lakes Forecasting System, Ohio State University/NOAA Great Lakes Environmental Research Laboratory). In light of the considerable differences in trophic state between the basins, different patterns of water movement from the eastern and western basins to the central basin may have partly contributed to observed intra-basin variability.

In Lake Ontario, there were differences in species composition of the summer zooplankton community between the eastern and western portions of the lake. Most notably, the cladoceran community in the west was dominated by *B. longirostris*, while the community in the east was dominated by *D. retrocurva*. The predatory *C. pengoi* was only found at stations where *D. retrocurva* was dominant, and it is tempting to hypothesize that predation by *C. pengoi* might have caused a shift from *B. longirostris* to the larger bodied *D. retrocurva*. However, there were other differences between eastern and western stations. The rotifer *Polyarthra vulgaris* was dominant in the west of the lake but nearly absent from the east, where *Ascomorpha ovalis* was the dominant rotifer (Barbiero and Tuchman 2000). Also, thermal structure was more strongly developed at eastern stations than in the west (Barbiero and Tuchman 2001b), and patterns of integrated current velocity during the summer survey suggested two circulation cells that coincided in large part with the two different communities. Patalas (1969), in an extensive study of spatial heterogeneity of Lake Ontario, showed that over a seasonal period populations of most species in the lake develop first in the east and subsequently move west. Therefore, if *B. longirostris* preceded *D. retrocurva*, as in fact was the case in Patalas' study, the difference in distribution could have been due to differences in population timing, rather than invertebrate predation. Johannsson (1987) similarly found increased *B. longirostris* populations, accom-

panied by concomitant decreases in *D. retrocurva*, in the western part of the lake in 1982. This was attributed to slower growth of *D. retrocurva* due to decreased temperature resulting from upwelling events in the western end of the lake, and perhaps also to a decrease in predation pressure due to cooler temperatures.

Community Composition by Lake

The observed dominance of the offshore community in Lake Superior by large calanoid copepods is consistent with findings from the early 1960s through the early 1980s (Olson and Odlaug 1966, Swain *et al.* 1970, Patalas 1972, Schelske and Roth 1973, Conway *et al.* 1973, ULRG 1977, Watson and Wilson 1978, Sprules and Jin 1990) and suggests there has been little change during this time. Five species are known to exist in the lake year round: *L. macrurus*, *L. sicilis*, *L. ashlandi*, *Seneccella calanoides*, and *D. thomasi* (Selgeby 1975, Watson and Wilson 1978), and these species comprised 99.9% of the spring zooplankton community. Summer communities in Lake Superior are unusual in their relative paucity of cladocerans, compared to the other Great Lakes. Sprules and Jin (1990) reported a 20% contribution of cladocerans to summer biomass in both 1973 and 1983, and in this study their contribution was similarly low (approximately 10%). Offshore densities of cladocerans, however, have been shown to increase in late summer, when populations apparently expand from in-shore regions (Watson and Wilson 1978). It is possible, therefore, that the samples collected in this study, which were taken in late August, missed this population maxima. Co-dominant cladocerans in the present study were *Holopedium gibberum* and *Daphnia galeata mendotae*. While usually noting the presence of *H. gibberum*, previous studies have typically listed either *Bosmina* (primarily *B. longirostris*) or *Daphnia* (primarily *D. galeata mendotae*) as the dominant cladoceran in the lake (Swain *et al.* 1970, Patalas 1972, Schelske and Roth 1973, Selgeby 1975, Watson and Wilson 1978).

Lakes Michigan and Huron showed remarkable similarity in their zooplankton communities in terms of both species composition and abundance during spring and summer. The recent history of the zooplankton community has been particularly well documented in Lake Michigan. Prior to 1982, planktivory by alewife resulted in an offshore zooplankton community dominated by the calanoid copepods *L. ashlandi* and *L. minutus*, with clado-

cerans, represented primarily by the relatively small *D. retrocurva*, a minor component (Scavia *et al.* 1986, Evans and Jude 1986). The collapse of the alewife population in 1982 led to a dramatic shift in the composition of the offshore zooplankton community towards dominance by cladocerans, initially the very large *Daphnia pulicaria*, but subsequently a three species complex consisting of *D. pulicaria*, *D. galeata mendotae* and *D. retrocurva*. After the introduction to the lake of the predatory *Bythotrephes* in 1986, the offshore zooplankton community shifted back to a community dominated by diaptomid calanoids (*L. ashlandi*, *L. sicilis* and *L. minutus*), with cladocerans represented almost exclusively by *D. galeata mendotae*. This community appears to have been fairly stable during the early 1990s (Makarewicz *et al.* 1995), and the community in 1998 was essentially similar to that reported by these authors.

Considerably less information is available on open water zooplankton communities in Lake Huron. Watson and Carpenter (1974) found that in 1971 calanoid copepods made up 17 and 43% of August and September crustacean densities, respectively, with diaptomid copepodites contributing the majority of individuals in both cases. Cyclopoid copepodites contributed 42 and 35% of individuals on those dates. Evans (1986) similarly found substantial numbers of both diaptomid copepodites (40% non-nauplii crustaceans) and cyclopoid copepodites (27%) in 1980, while diaptomids made up 44% of crustacean abundance in August, 1988 (Sprules and Jin 1990). Dominant diaptomid species, when specified, have most often been *L. minutus* and *L. ashlandi*. While the presence of diaptomids during the summer seems to have been fairly constant in that past 30 years, there appears to have been a shift in the cladoceran community. Prior to 1988, bosminids are consistently cited as the dominant cladocerans, with daphnids typically contributing less than 10% to crustacean densities (Patalas 1972, Watson and Carpenter 1974, Korstad 1983, Evans 1986). In 1988, however, daphnids made up 22% of the summer crustacean community, compared to a contribution by bosminids of 14% (Sprules and Jin 1990). The data in this study indicate a similar dominance by daphnids (25%) in comparison to bosminids (8%). The shift in the cladoceran community toward larger species could be indicative of either a release from vertebrate predation pressure, or an increase in invertebrate predation. This shift seems to have coincided with the establishment of *Bythotrephes* in the lake in 1984

(Bur *et al.* 1986), but while *Bosmina* is a known prey item of *Bythotrephes* (Monakov 1972, Vanderploeg *et al.* 1993), Branstrator and Lehman (1991) reported an increase in *Bosmina* populations in Lake Michigan after the establishment of *Bythotrephes*, arguing this was the result of coincident decreases in *Leptodora* populations. While the change in cladoceran community structure in Lake Huron bears some similarities to that seen in Lake Michigan, a more detailed examination of cladoceran communities before and after the establishment of *Bythotrephes*, along with fish population data, would be necessary to determine whether such changes resulted from similar causes.

Lake Erie was unique among the lakes both for its high species richness and the degree of difference in species composition between its different basins. Among the species found exclusively or predominantly in Lake Erie were a number of organisms commonly found in warm, shallow, and/or more productive environments. *Leptodiptomus siciloides*, which was the dominant diaptomid in the western basin, is a form more commonly associated with ponds or shallow lakes (Balcer *et al.* 1984) and is considered a eutrophic indicator. Both *S. oregonensis* and *E. affinis* were found in substantially greater numbers in Lake Erie than in the other lakes. *Eurytemora affinis*, a marine invader first noted in the Great Lakes in Lake Ontario in 1958 (Anderson and Clayton 1959) was also found in that lake in small numbers; in Lake Erie it was restricted to the western basin. *Skistodiptomus oregonensis*, while found in limited numbers in all the lakes except Superior, was the overwhelmingly dominant calanoid in the central basin of Lake Erie. Among the cyclopoids, the warm water forms *M. edax*, *T. prasinus mexicanus*, and *A. vernalis* were either absent or found only rarely in the other lakes. All three achieved their maximum densities in the western basin of Lake Erie.

Due to its shallowness, Lake Erie was the most significantly impacted of the Great Lakes by the acceleration of eutrophication seen in the last century. Among the changes in the zooplankton community associated with eutrophication have been a decrease in the dominance of calanoid copepods, an expansion of the ranges of warm-water, eutrophic species such as *C. sphaericus*, *L. siciloides*, *L. minutus*, *S. oregonensis*, and *A. vernalis*, and decreases in the populations of the deep-living copepods *L. macrurus* and *L. sicilis* (see review in Johannsson *et al.* 1999). With the institution of phosphorus controls

in the 1970s, some of these trends appear to be reversing.

Recently, the relative composition of the community appears to be shifting more toward calanoid copepods (Johannsson *et al.* 1999). During the period 1983 to 1987, values of the ratio of calanoids to (cyclopoids + cladocerans) averaged 0.27, 0.58, and 0.69 for the western, central, and eastern basins, respectively, for April and August samples (Makarewicz 1993). These values represent statistically significant increases over those seen in 1970 (Johannsson *et al.* 1999). This ratio is thought to provide an indication of trophic state, with higher values indicating more oligotrophic conditions (Gannon and Stemberger 1978). Values of this ratio from the present study (0.35, 0.86, 0.63 for western, central, and eastern basin, respectively) indicate that the shift observed in the 1980s toward increasing calanoid dominance is continuing in the lake.

Some apparent changes in species distributions have also been seen since the institution of phosphorus controls. Notably absent from Lake Erie in the present study was the small cladoceran *C. sphaericus*. This organism, generally associated with eutrophic environments (Balcer *et al.* 1984), was commonly reported from the lake during the 1950s and 1960s (Davis 1954, Davis 1962, Britt *et al.* 1973), although its distribution has more recently (1983 to 1987) been restricted to the western basin (Makarewicz 1993). Its absence from the open water in the present study might be taken as further evidence of improvement in the nutrient status of the lake. Another species typical of warmer, high productivity environments is *L. siciloides*. It was first noted in the lake in 1929 (Beeton 1965), and its populations increased substantially beginning in the 1940s (Davis 1966). In 1967 Davis (1968) reported it to be common in all three basins of the lake, although it was most abundant in the western basin. During 1983 to 1987, *L. siciloides* was reported from both the western and eastern basins (Makarewicz 1993). In this study it was almost entirely restricted to the western basin.

Populations of the glacial relict calanoid *L. macrurus*, however, have apparently not recovered in the lake. This species was widely distributed throughout the lake at one time, and although it was confined to the deeper sections during the warm summer months, it was extremely abundant at these stations, comprising up to 74% of the total crustacean fauna (Fish and Assoc. 1960). Davis (1954) reported that *Limnocalanus* was common in Cleveland Harbor during 1951 to 52; however he failed

to find any when sampling the same area in 1956 to 57 (Davis 1962) or during a lake wide survey in 1967 (Davis 1968). Gannon and Beeton (1971), documenting the decline of *Limnocalanus* in Lake Erie since the late 1920s, blamed it on hypolimnetic oxygen depletion and increased fish predation.

In the present study, *Limnocalanus* was restricted to the western basin in spring, where it made up approximately 10% of individuals in the basin. In summer *Limnocalanus* was only found in the central basin, and at extremely low densities. Gannon and Beeton (1971) reported a similar distribution in the lake in 1957, with low densities in the western basin in May and June and extremely low densities in the central basin in July and the eastern basin in August. This distribution led them to suggest these were transient populations immigrating from Lake Huron via the St. Clair and Detroit rivers, which was probably also the case in this study.

The crustacean community in Lake Ontario differed from the other Laurentian Great Lakes in that it was overwhelmingly dominated by cyclopoid copepods and cladocerans, with calanoid copepods making up only a minor component of the zooplankton community. For example, immature diaptomids accounted for only 1% of summer crustacean abundance in Lake Ontario, compared to 21% in Lake Erie, 29% in Lakes Michigan and Huron, and 55% in Lake Superior. Summer communities were instead dominated by *D. thomasi* and either *B. longirostris* or *D. retrocurva*, depending on location. While McNaught and Buzzard (1973) speculated that diaptomids and *Daphnia* species figured more prominently in communities earlier in the last century, the current community composition seems to have been very stable at least since the mid 1960s (Patalas 1969, Watson and Carpenter 1974, McNaught *et al.* 1975, Taylor *et al.* 1987, Sprules and Jin 1990, Johannsson *et al.* 1991). While Patalas (1972) attributed summer dominance patterns to eutrophication of the lake, more recent studies (Taylor *et al.* 1987, Sprules and Jin 1990) have pointed to the importance of intense planktivory, particularly by alewives, in structuring the zooplankton community. This is consistent with the lack of large calanoids, and the high densities of *B. longirostris* and *D. thomasi*, both of which are less susceptible to fish predation than other species (Brandt 1980, Taylor *et al.* 1987). Johannsson (1987) pointed out that neither reductions in phosphorus loading nor stocking of piscivorous fish has had any detectable effect on the zooplankton community between 1967 and 1982.

Lake to Lake Differences

Results from DCA analyses indicated that each lake supported very distinct summer crustacean communities, with the notable exception of Lakes Michigan and Huron whose communities were virtually identical. In Patalas' (1975) classification of North American great lakes, Lakes Superior and Huron were grouped together on the basis of high species number, low densities, and communities dominated by the two diaptomids *Leptodiatomus sicilis* and *Leptodiatomus ashlandi*, *Diacyclops thomasi* and *L. macrurus*, while Lakes Erie and Ontario were grouped on the basis of intermediate species number, high densities, and communities dominated by cyclopoid copepods and the cladocerans *B. longirostris*, *D. retrocurva*, and *D. galeata mendotae*. Lake Michigan was determined to be intermediate between the two groups. While obviously operating on a different scale of resolution, the data from this study suggest an emendation of the above classification, grouping Lakes Michigan and Huron together as daphnid/diaptomid lakes and separating Lake Superior on the basis both of low densities and community dominance primarily by larger calanoids (e.g., *L. sicilis*, *L. macrurus*).

Judging from their positions in the DCA ordination, summer communities in the central and eastern basins of Lake Erie showed as much or more affinity for those in Lakes Michigan and Huron than for communities in Lake Ontario, and indeed for those in the western basin of Lake Erie. It also appeared that distinctions between communities in the upper lakes and Lake Erie (excluding the western basin) were relatively independent of both total phosphorus and chlorophyll concentrations. Instead, DCA ordination suggested that physical factors, e.g., temperature and depth, were more important in separating these communities from each other than were phosphorus or chlorophyll. The prominent influence of abiotic factors in structuring the zooplankton communities in these systems has been pointed out by previous authors. Patalas (1975) has shown the association between both mean depth and epilimnetic temperature and species number in his comparative study of North American great lakes. More recently, Fahnenstiel *et al.* (1998) interpreted the similarity in structure of microorganism communities in the Great Lakes as evidence of the strong influence of abiotic factors. Communities in the western basin of Lake Erie and in Lake Ontario appeared to be distinguished from those in the other lakes at least in part by differences in total phos-

phorus and chlorophyll, according to ordination analysis. Even so, these communities were very different from each other, and indicate that other factors modified the effects of trophic state on zooplankton community composition in these two areas. It should be borne in mind that this evaluation of the factors responsible for the ordination results did not consider some potentially important factors. Most notably, the level of planktivory, vertebrate or invertebrate, was not examined, and this would obviously have an impact on determining zooplankton community structure.

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